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PARALLEL BEHAVIORAL DIVERGENCE WITH MACROHABITAT IN *ANOLIS* (SQUAMATA: DACTYLOIDAE) LIZARDS FROM THE DOMINICAN REPUBLIC

KATHERINE E. BORONOW,¹ IAN H. SHIELDS,² AND MARTHA M. MUÑOZ^{3*}

ABSTRACT. The ecomorph concept of the adaptive radiation of Caribbean anoles is characterized by a suite of behavioral, ecological, and morphological traits that are tightly linked to microhabitat use in lizards. However, most studies on the adaptive radiation of anoles have been conducted in a single macrohabitat type—lowland tropical forests. Because behavior can help organisms cope with different environmental conditions, we can predict that there will be key shifts in behavior within ecomorphs when examined across different macrohabitats, although this idea remains empirically underexplored. Here we utilized the replicated evolution of montane endemics from a primarily lowland species in a clade of trunk-ground *Anolis* lizards to test the hypothesis that shifts in basking behavior, wariness, and display behavior accompany divergence into montane habitats. The montane specialists *A. armouri* and *A. shrevei* each independently evolved from the primarily lowland dwelling *A. cybotes* in two widely separated mountain chains on the island of Hispaniola. We found evidence for a convergent behavioral response to the high-altitude macrohabitat: *A. armouri* and *A. shrevei* spend more time basking, utilize more open environments, and are warier than lowland *A. cybotes*. We also found divergence in display behavior in *A. shrevei*. We detected no evidence of divergence in locomotor behavior with elevation among active lizards. Together, our results suggest that the ecomorph concept would be enriched by extending observations of behavior (and other aspects of the phenotype) into different macrohabitats. Future work should focus on whether the observed behavioral shifts are clinal, reflecting local adaptation within *A. cybotes*, or fixed differences between the lowland generalist and montane species. Adaptation to the macrohabitat has previously been underappreciated as a source of behavioral diversity in *Anolis* lizards: this study is the first step toward documenting intraecomorph behavioral variation across divergent habitats.

KEY WORDS: *Anolis*; display; flight initiation distance; macrohabitat; thermoregulation

¹ Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A.; e-mail: katherine.boronow@gmail.com.

² UT Southwestern Medical Center at Dallas, Dallas, TX 75390, U.S.A.; e-mail: ianhshields@gmail.com.

³ Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia 24060; e-mail: mmunoz5@vt.edu.

INTRODUCTION

Organisms entering novel macrohabitats (i.e., environments that differ markedly in factors such as climate, soil or water chemistry, vegetation cover, or a combination of factors) must adapt to a suite of differing

environmental conditions with physiological, morphological, or behavioral changes. Studies on phenotypic divergence across macrohabitats have typically focused on physiological divergence (Gaston and Chown, 1999; Givnish et al., 2004; Barrett et al., 2011) and morphological divergence (Smith et al., 1997; Ogden and Thorpe, 2002; Langerhans et al., 2003); evidence for behavioral divergence, however, remains comparatively understudied (but see Kirschel et al., 2011; Kozlovsky et al., 2014; Muñoz and Losos, 2018). Studies of behavioral divergence across elevation are particularly useful in the light of climate change, because habitat tracking will push organisms into novel macrohabitats, unless the macrohabitats themselves migrate (e.g., as with forest trees) (Larsen, 2012; Frishkoff et al., 2015).

Species occupying altitudinal gradients are excellent models for studying adaptation to environmental variation. Altitudinal gradients are characterized by dramatic shifts in macrohabitat: climatic factors structure plant communities into a series of biomes (Körner, 2007; Martin et al., 2011), and these biomes support unique animal communities. Species that are found along wide elevational gradients are either composed of generalist populations (each adapted to a wide range of conditions) or of populations that are specialized to their local conditions.

The Caribbean radiation of *Anolis* lizards is well known for the replicated evolution of microhabitat specialists, termed ecomorphs, on islands in the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico) (Williams, 1983; Losos et al., 1998). Members of each ecomorph are characterized by their convergent morphology and structural microhabitat use (e.g., twig, tree trunk, grass) (Williams, 1983; Losos et al., 1998; Mahler et al., 2013). Species within an ecomorph category also share behavioral adaptations to structural microhabitat: loco-

motor behavior, foraging mode, and territorial overlap are all associated with ecomorph type (Moermond, 1979; Losos, 1990; Johnson et al., 2008, 2010). Ecomorph members do not, however, converge in climatic preferences or requirements (Ruibal, 1961; Rand, 1964a; Williams, 1972; Hertz et al., 2013). Rather, members of each ecomorph have diversified to inhabit a broad range of macrohabitats. By examining behavioral divergence *within* an ecomorph class across a wide altitudinal range, we can broaden our understanding of ecomorph evolution, which has most often focused on between-ecomorph divergence.

The cybotoids—a clade of trunk-ground anoles from the Caribbean island of Hispaniola—have the greatest altitudinal distribution of any Caribbean *Anolis* lineage, as they are found from sea level to over 3,000 m (Schwartz, 1989; Glor et al., 2003) and therefore occupy a wide range of macrohabitats. In this study, we focus on the occupants of the altitudinal extremes: *Anolis cybotes* from lowland mesic forest and *A. shrevei* and *A. armouri* from high-altitude pine forest in the Cordillera Central and Sierra de Baoruco, respectively. *Anolis shrevei* and *A. armouri* are phylogenetically nested within *A. cybotes* (Glor et al., 2003; Wollenberg et al., 2013), each predicted to have evolved independently from an ancestor ecologically and morphologically similar to *A. cybotes*. Thus, *A. shrevei* and *A. armouri*, which occupy widely separated mountain chains, each represent an evolutionarily independent replicate of adaptation to high elevation from a low-elevation ancestor. Each montane cybotoid is more closely related to the lowland form of *A. cybotes* from its own mountain range than either lowland population is to each other (Glor et al., 2003; Wollenberg et al., 2013). Previous work in this clade found that environmental variation—particularly in macrohabitat, rather

than structural microhabitat—partly explained morphological variation among *A. shrevei*, *A. armouri*, and *A. cybotes* (Wollenberg et al., 2013). This study also found that the morphological differentiation occurred in parallel across the two mountain chains, suggesting an adaptive basis to the morphological shifts (Wollenberg et al., 2013). Here, we test the hypothesis that a diverse suite of behavioral traits has also accompanied the divergence of *A. shrevei* and *A. armouri* into a high-altitude environment.

Montane cybotoids are known to compensate behaviorally for the colder environments at high elevation by increasing their basking behavior (i.e., by spending a greater proportion of time in sunlight rather than shade) (Hertz and Huey, 1981; Muñoz et al., 2014; Conover et al., 2015). Increased basking behavior is thought to result from lizards utilizing more exposed and open perches at high elevation (Hertz and Huey, 1981; Muñoz et al., 2014; Conover et al., 2015; Muñoz and Losos, 2018), but actual perch characteristics have not been formally quantified. We had two main goals for this study. First, we quantified the “openness” of lizard perches using three features of structural habitat: percent ground cover, percent canopy cover, and vegetation height of the nearest perch. Second, we tested the hypothesis that, because of their use of more open habitats, montane lizards are divergent from lowland lizards in three key behavioral dimensions: escape behavior (flight initiation distance), display behavior (dewlap and pushup rate), and locomotor behavior (movement types and rates), with directional hypotheses described below.

Flight initiation distance (FID)—the distance at which an animal flees from an approaching predator—is often higher (meaning lizards will flee when the threat is farther away) in more open habitats (Martín and López, 1995; Schulte et al., 2004; Cooper

and Wilson, 2007). FID is also typically inversely correlated with body temperature in ectotherms (Rand, 1964b; Rocha and Bergallo, 1990; Smith, 1997; Cooper, 2000), but mean daytime body temperature in montane cybotoids is quite similar to low-elevation lizards (Muñoz and Losos, 2018). Because lizards at high elevation are thought to utilize more open perches, we predicted that flight initiation distance would be greater in montane habitats.

Anolis lizards engage in visual displays using colorful, extensible throat fans (termed dewlaps). These displays, while enabling social communication, can also make lizards more vulnerable to predators by making them more conspicuous (Stuart-Fox et al., 2003). Indeed, in the presence of predators, *Anolis sagrei* reduces the conspicuousness of its displays by decreasing the amplitude of their head-bobs (Steinberg et al., 2014). Anoles that rely heavily on crypsis to avoid predation exhibit fewer movements (Johnson et al., 2010). Movement rates in anoles vary according to microhabitat use (Cooper, 2005) and risk of predation (Lima, 1998; Hawlena and Pérez-Mellado, 2009; Zani et al., 2013). On the basis only of increased vulnerability to predation in more open habitats, we would expect montane lizards to perform fewer dewlaps and pushups and exhibit more cryptic behavior (i.e., fewer movements per minute) than their lowland counterparts. We test these hypotheses in two mountain chains occupied by independently evolving taxa and predict divergence in behavior to occur in parallel across sites.

MATERIALS AND METHODS

Study sites

We conducted our study in the Dominican Republic, Hispaniola, during June and July 2012. We worked at four study sites,

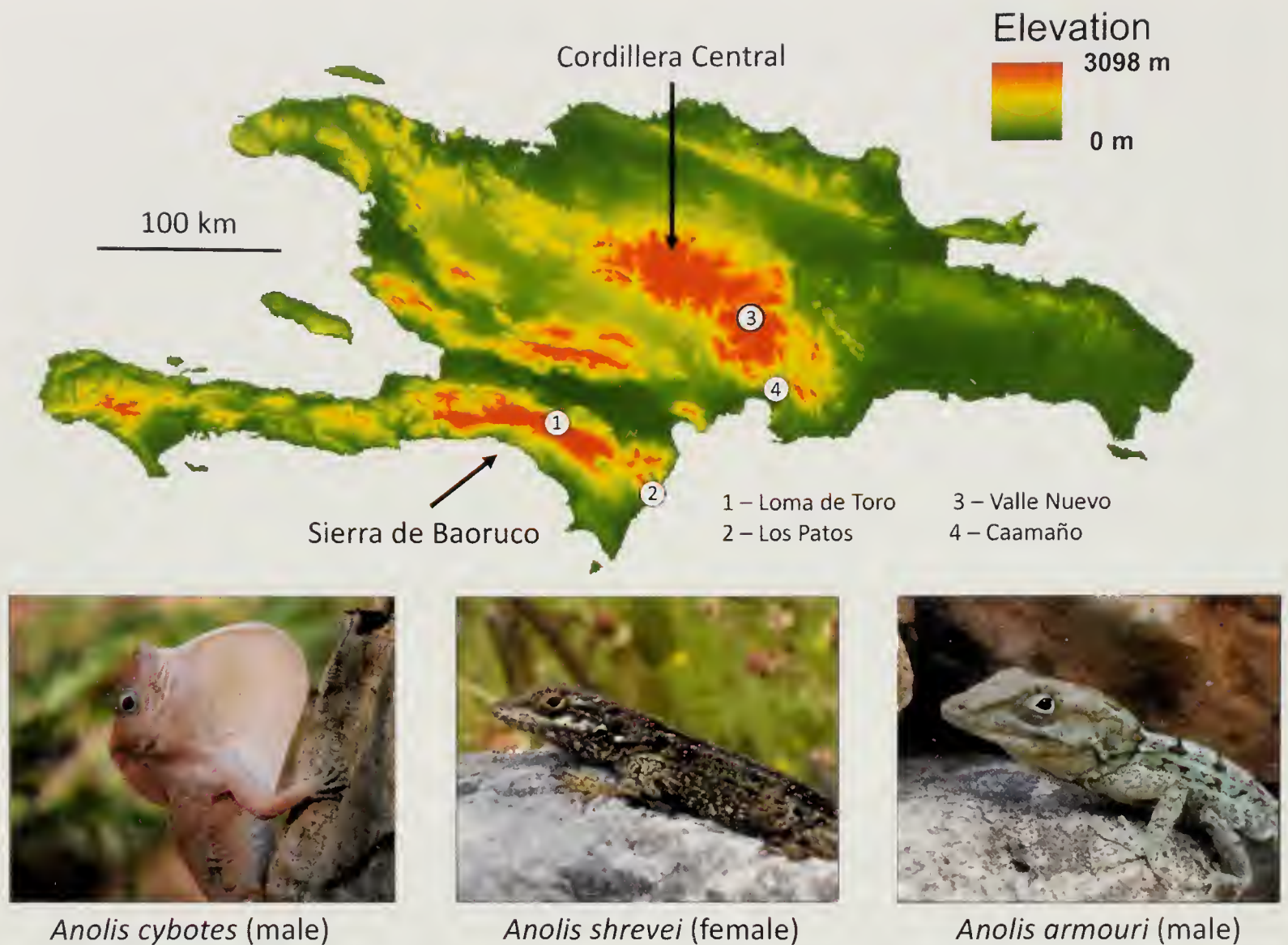


Figure 1. Map showing the island of Hispaniola, with the sites for this study numbered. The three images show *Anolis cybotes*, *A. shrevei*, and *A. armouri*. *Anolis cybotes* is found in the two lowland sites (Los Patos and Caamaño). *A. shrevei* is found at high elevation in the Cordillera Central (Valle Nuevo), and *A. armouri* is found at high elevation in the Sierra de Baoruco (Loma de Toro). Map provided by V. Farallo. Photo of *A. cybotes* by Duncan Irschick

consisting of a low- and high-elevation site in each of two mountain chains: The Sierra de Baoruco (SB), located in the southwestern region of the Dominican Republic, and the Cordillera Central (CC), located in the central Dominican Republic (Fig. 1). In both of these mountain ranges, freezing temperatures and the increased frequency of fires prevent expansion by tropical tree species above approximately 2,200 m, and the vegetation type switches from montane cloud forest to a monodominant pine forest (Martin et al., 2011). In contrast, broadleaf hardwood species dominate at lower elevations.

Study sites in the SB were located near Los Patos, Barahona Province (13 m above sea level; 17°57'18"N, 71°11'17"W) and Loma del Toro, Sierra de Baoruco National Park, Independencia Province. At Loma del Toro, separate sites were used for the behavioral observations (2,009 m above sea level; 18°17'32"N, 71°41'52"W) and flight initiation distance measurements (2,258 m above sea level; 18°17'15"N, 71°42'45"W) because of time constraints and the limited availability of suitable habitat at a single elevation. However, these sites were not qualitatively different in macrohabitat characteristics. Study sites in the CC were located near Francisco Alberto Caamaño Deñó National

Park, Azua Province (43 m above sea level; 18°26'07"N, 70°35'33"W) and Valle Nuevo National Park, La Vega Province (2,450 m above sea level; 18°43'48"N, 70°36'00"W).

Both low-elevation sites were occupied by *A. cybotes* in semidisturbed habitats that were located within or adjacent to mesic forests (Fig. 1). The majority of lizards in Los Patos (SB) were observed in minimally maintained stands of coconut and plantain. Lizards in Caamaño National Park (CC) were observed on a variety of tropical hardwood trees and man-made perches (e.g., fence posts). Loma del Toro (SB) was occupied by *A. armouri*, and Valle Nuevo National Park (CC) was occupied by *A. shrevei* (Fig. 1). Lizards in both high-elevation sites used clearings and edges surrounded by pine forest. Low- and high-elevation sites differ considerably in mean annual, maximum, and minimum temperatures, with low-elevation sites being much warmer than high-elevation sites (Table 1). The geographic locations of these populations in the context of the available phylogenetic data suggest that, in each transect, the low- and high-elevation populations are more closely related than the lowland *A. cybotes* populations are to each other (Glor et al., 2003).

Habitat openness

To assess habitat structure, we collected data on vegetation at each individual's initial

perch site in the flight initiation distance trials. Canopy cover was estimated using a spherical densiometer (Lemmon, 1956). Ground cover was recorded within a 2-m-diameter circle centered at the perch site. Visual estimates of percent cover were made for five categories: bare earth, rock, litter (vegetative debris), herbaceous plants, and woody plants. Finally, height of the nearest vegetation to the lizard's initial perch was measured. All measures of the environment were taken by the same researcher (K.E.B.) and are similar measures to those employed by Melville and Swain (2000) and Gifford et al. (2008). We combined the percent cover of bare earth and rock to create an index of exposed substrate. Canopy cover and exposed substrate were arcsine square root transformed, and height of the nearest vegetation was natural log transformed before analysis.

Behavioral observations

Behavioral observations were conducted on adult male lizards over a period of 2–3 days per site following the methods of Johnson et al. (2010). We chose to focus on males to observe display behavior while avoiding sex-based differences in our data. We located undisturbed individuals by walking slowly through the habitat and surveying the vegetation. Individuals were sexed at a distance using binoculars on the basis of

TABLE 1. TEMPERATURE PROFILES OF THE FOUR STUDY SITES.^a ALL TEMPERATURES ARE GIVEN IN DEGREES CELSIUS.

Mountain range	Elevation	Mean annual temperature	Maximum annual temperature	Minimum annual temperature	Mean observed temperature
Cordillera Central	low	24.8	30.9	17.9	29.3
	high	10.1	17.5	1.8	22.1
Sierra de Baoruco	low	26.0	32.2	19.3	30.5
	high	13.9	21.1	5.4	19.1

^aMean, maximum, and minimum annual temperatures of the study sites were extracted from the WorldClim database (Hijmans et al., 2005) via ArcMap 10.

diagnostic differences in size, head shape, and dorsal patterning (Schwartz, 1989). Behavior was either recorded during observations in the field or subsequently scored in the lab on the basis of videotapes of the lizard. We did not observe any systematic differences in mean behavioral variables between field-recorded and videotaped observations, suggesting that these two methods provided comparable results. To ensure that the observation period offered each lizard adequate time to engage in a normal range of behaviors, only individuals for which behavioral observations exceeded 30 min were retained. As a result, the length of observations per animal ranged from 30 to 64 min. Observations were conducted when lizards were active, between 0730 and 1800 h. We did not conduct observations during rainy conditions. To avoid observing the same individual multiple times, we caught each lizard at the end of the observation period and held it until all the observations were complete. Because each locality contained many more individuals than were observed in this study, sequentially removing lizards was unlikely to have significantly diminished the social environment for lizards observed later in each site. Additionally, any effect of lizard removal on behavior should be similar across sites.

Display behavior

For each behavioral observation, we counted all dewlap extensions (each time the dewlap was extended away from the body) and pushups (each time the upper body or head was elevated from the ground). Head-bobs were grouped with pushups because the two movements are difficult to distinguish during observation. We also recorded the total duration of display during the observation period.

From these data, we calculated the proportion of time spent displaying (display time/observation time), pushup rate (number of pushups/display time), and dewlap rate (number of dewlaps/display time). Dewlap rate and pushup rate were natural log transformed and the proportion of time spent displaying was arcsine square root transformed to meet the requirements for parametric analysis.

Locomotor behavior

During behavioral observations, we also recorded locomotor activity. We recorded all movements as walks, runs, or jumps. From these data, we calculated movements per minute (MPM, which was calculated as the sum of walks, runs, and jumps, which were then divided by the length of the observation period) and walk, run, and jump frequency (calculated as a proportion of all movements). Following Losos (1990) and Johnson et al. (2008), we excluded inactive lizards (MPM < 0.20) from analysis of MPM and locomotor frequencies. MPM was natural log transformed before analysis.

Basking behavior

During each observation, we also recorded the basking status of the lizard following established methods (Hertz, 1992). Basking status was divided into four categories: full sun, partial sun, shade, or overcast. Partial sun indicated that the lizard was partly in full sun and partly in shade or that the lizard was in sunlight that was being filtered through clouds. Overcast conditions were noted when the sun was completely obscured by clouds. From these data, we calculated the percentage of time spent basking (time in full and partial sun/total nonovercast time) and the proportion of overcast conditions (time overcast/observation period). Time spent basking excluded

overcast conditions because lizards were unable to select basking sites during these periods.

Escape behavior

To assess escape behavior, we measured FID. We walked slowly through the study area until locating an undisturbed adult male lizard. Following established methods, one of the investigators (K.E.B.) approached the lizard, simulating a predation threat (Martín and López, 1995; Cooper, 2000). The investigator approached the lizard from the front or side, depending on the orientation of the lizard and the available walking routes, at a calibrated speed of 1.45 ± 0.04 m/s (mean \pm SD) until the lizard fled its initial position. To minimize variation in the stimulus, the investigator wore similar, neutral-colored clothing for all trials.

We measured the horizontal distance between the investigator at the point at which the lizard fled and the lizard's initial location (i.e., FID). We also measured the substrate temperature at the lizard's initial position with a noncontact infrared thermometer (MiniTemp MT6, Raytek Corporation, Santa Cruz, California) from a distance of less than 25 cm from the substrate. Substrate temperature was used as a proxy for internal body temperature because the majority of lizards escaped to refuges where they could not be pursued; as such, their body temperature could not be measured. Substrate temperature relates positively with body temperature in *Anolis* lizards, although the correlation may not be strong (Heatwole et al., 1969). Air temperature was also recorded using a thermocouple (Type T, copper constantan, Omega Engineering Inc., Stamford, Connecticut) connected to a temperature logger (HH603A, Omega).

All trials at a given site were conducted over 2–3 days between 0900 and 1630 h. FID trials were conducted concurrently with behavioral observations at both sites in the CC. Investigators canvassed different areas of the site at different times to avoid disturbing each other; however, it is possible that a lizard tested for FID was subsequently observed for basking and display behavior. To avoid testing the same individual for FID multiple times, each area within a site was surveyed only once. Because male *A. cybotes* are territorial and have small home ranges (Johnson, 2007), it is unlikely that we tested the same individual multiple times at a single site. We did not conduct trials during inclement weather. FID was natural log transformed before analysis.

Analyses

Mountain chain and elevation often interacted to determine the behavioral or environmental pattern. We therefore decided to perform separate analyses for each mountain chain to improve our ability to interpret how behavior and environment vary with respect to elevation, our main variable of interest. Additionally, although we hypothesized that the altitudinal trends in behavior would be similar between the mountain chains, finding dissimilar patterns of variation would not be surprising given their unique biogeographical histories and independent speciation events.

To summarize habitat structure, we performed a principal component analysis (PCA) on the correlation matrix of canopy cover, height of the nearest vegetation, and exposed substrate. We then tested for differences in habitat with elevation by performing Welch's two-sample *t*-test on PC1, PC2, and air temperature.

We used the Wilcoxon rank sum test to investigate whether the proportion of overcast conditions differed with elevation in

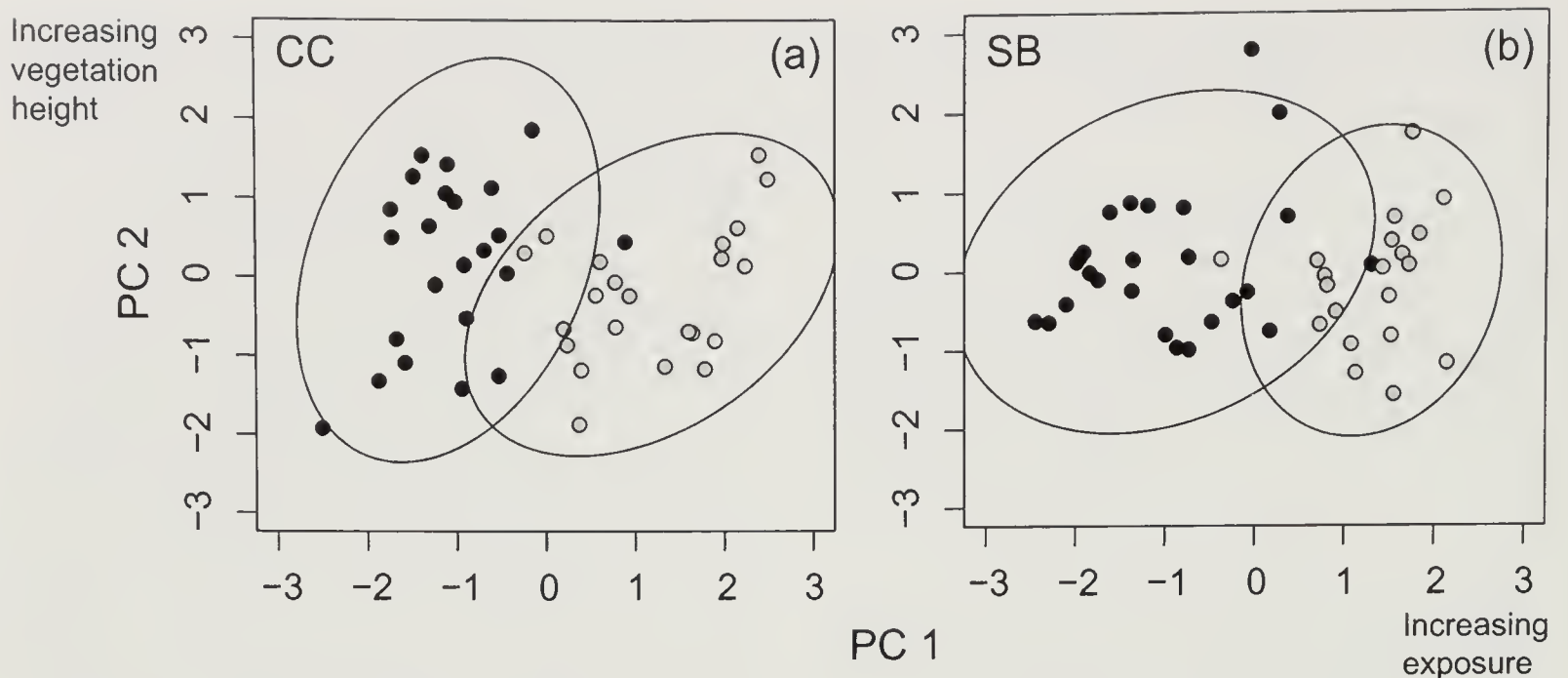


Figure 2. Principal component scores projected onto the first two principal component axes with a 95% confidence ellipse at low elevation (black circles) and high elevation (gray circles) in the Cordillera Central (a) and Sierra de Baoruco (b). Each point represents an individual lizard's perch site.

each mountain chain. To determine whether display and locomotor behavior differ with altitude, we used Welch's two-sample *t*-test to test for differences in percentage of time displaying, dewlap rate, pushup rate, and MPM between low and high elevation in both mountain chains. To determine whether the frequency of inactive lizards differed with elevation in each mountain chain, we used Fisher's exact test. To test whether FID differed with elevation, we used Welch's two-sample *t*-test. We also examined Pearson's correlation between FID and substrate temperature. All analyses were conducted in R (R Core Development Team, 2012).

RESULTS

Habitat structure

PCA revealed distinct differences in habitat matrix between high and low elevation (Fig. 2). In both mountain chains, we recovered two major axes that together explain 92.6% and 87.9% of the variation in the data in the CC and SB, respectively (Table 2). Patterns of loading in PC1 and PC2 were similar in both mountain chains: PC1 loaded most strongly for exposed substrate and canopy cover, with the two variables being oppositely weighted, whereas PC2 loaded most strongly for vegetation height (Table 2). In the SB, vegetation height

TABLE 2. PRINCIPAL COMPONENT ANALYSIS OF STRUCTURAL HABITAT DATA. THE RESPECTIVE LOADINGS OF EACH TRAIT ON PC AXES ARE GIVEN, WITH PERCENT VARIANCE EXPLAINED AND CORRESPONDING EIGENVALUES.

	Cordillera Central		Sierra de Baoruco	
	PC1	PC2	PC1	PC2
% Exposed substrate	0.91	-0.25	0.88	-0.12
% Canopy cover	-0.92	0.16	-0.81	0.48
Height of nearest vegetation	-0.41	-0.91	-0.71	-0.68
% Variance explained	62.1	30.5	64.4	23.5
Eigenvalue	1.86	0.91	1.93	0.71

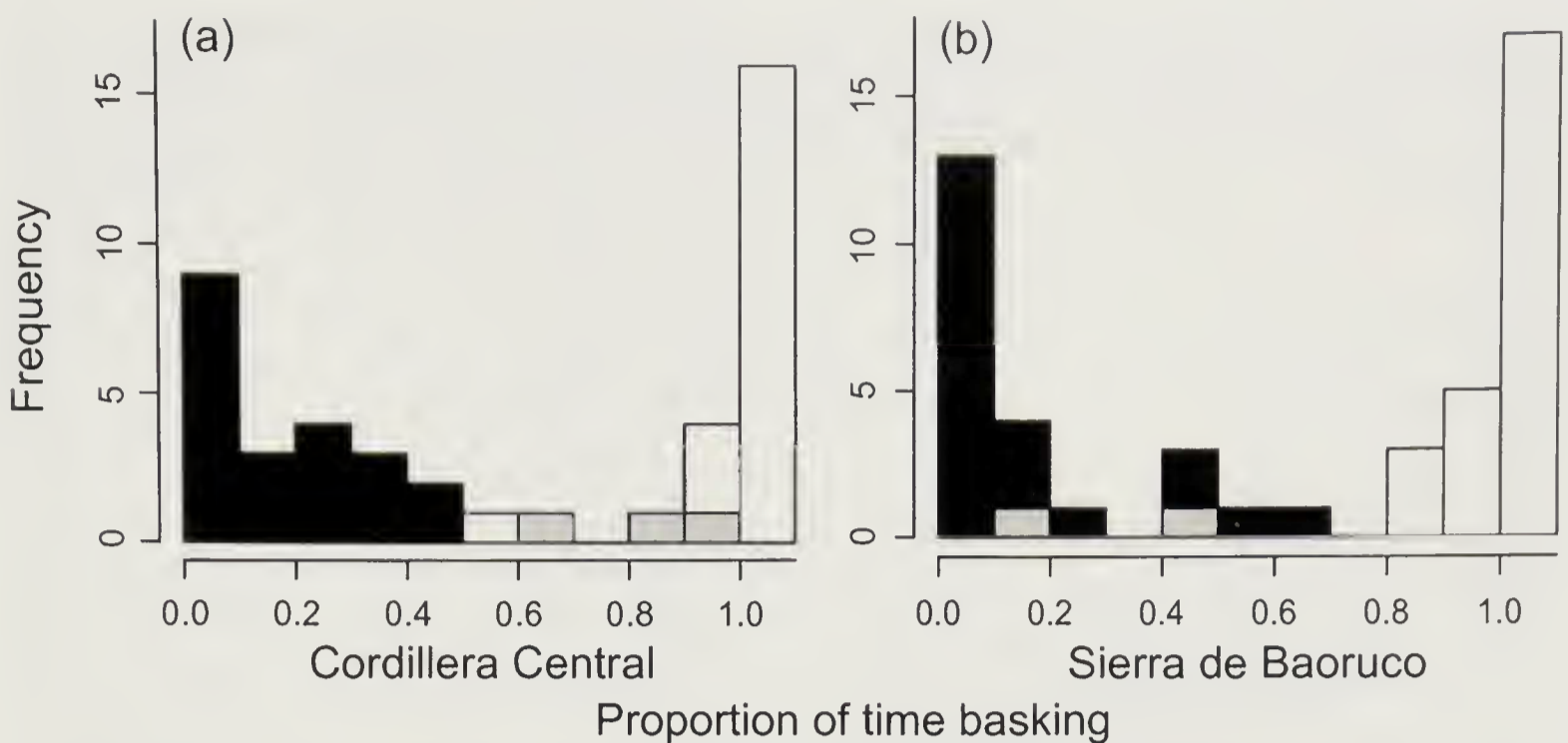


Figure 3. A histogram of the proportion of time spent basking at low elevation (black bars) and high elevation (white bars) in the Cordillera Central (a) and Sierra de Baoruco (b). Grey bars indicate overlap between the elevations.

also loaded strongly on PC1. High-elevation sites differed significantly on PC1 from low-elevation sites in both mountain chains (CC: $t = 9.84$, $df = 40.49$, $P < 0.001$; SB: $t = 10.04$, $df = 42.34$, $P < 0.001$), which indicates that the habitat matrix at high elevation contains more exposed substrate and less canopy cover. Additionally, in the SB, it indicates that vegetation height is somewhat lower at high elevation. However, sites did not differ in PC2 (CC: $t = 1.54$, $df = 43.25$, $P = 0.13$; SB: $t = 1.00$, $df = 42.73$, $P = 0.32$), indicating that vegetation height is not a primary driver of habitat differences. During our study, daytime air temperatures were colder at high elevation (CC: $t = 17.92$, $df = 32.32$, $P < 0.0001$; SB: $t = 38.17$, $df = 32.53$, $P < 0.0001$; Table 1).

Basking behavior

The proportion of time spent basking was much greater at high elevation in both the CC and SB (Fig. 3). In the CC, 87% of lizards basked more than 90% of the time at high elevation, whereas at low elevation,

88% of lizards spent at least half of their time in the shade. Similarly, in the SB, 81% of lizards basked for more than 90% of the time at high elevation, whereas at low elevation, 91% of lizards spent at least half of their time in the shade. This is not an artifact of sun availability, because the proportion of overcast conditions did not differ significantly between low and high elevation in either mountain chain (CC: $W = 321.5$, $P = 0.77$; SB: $W = 395$, $P = 0.29$). Additionally, lizards from all sites were sampled throughout the day, so sampling bias in the timing of observations did not affect this result.

Escape behavior

We obtained FIDs for 92 lizards ($n = 20$ – 26 individuals per site). In both the CC ($t = 5.79$, $df = 25.33$, $P < 0.001$) and the SB ($t = 5.64$, $df = 26.04$, $P < 0.001$), FID is much greater at high elevation, with lizards fleeing from the stimulus at a distance more than three times greater, on average, than that observed in lizards at low elevation (Fig. 4).

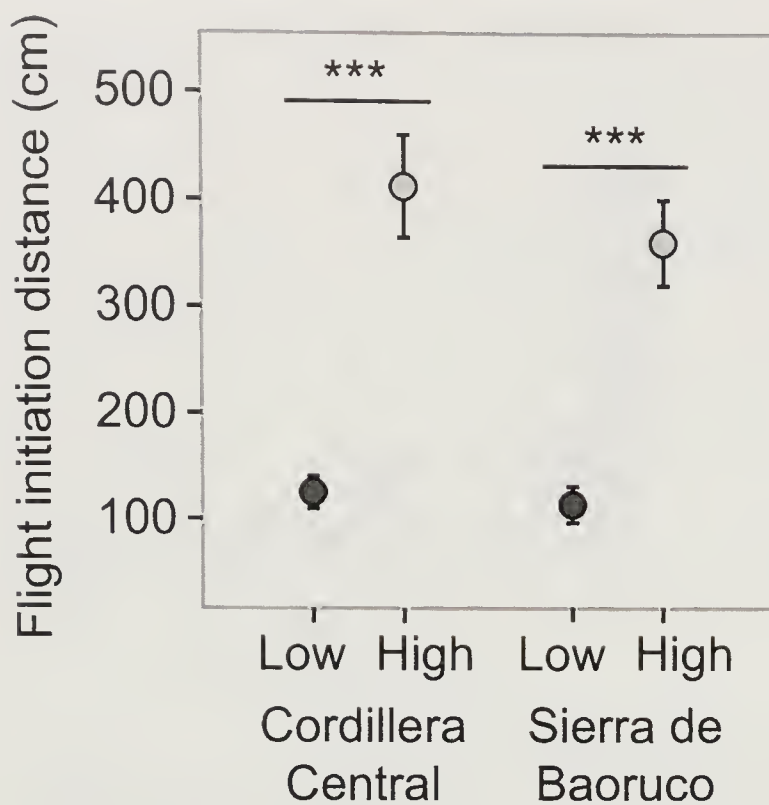


Figure 4. Mean flight initiation distance at low elevation (black circles) and high elevation (gray circles) in the Cordillera Central and Sierra de Baoruco. Error bars represent one standard error. *** $P < 0.005$.

Even though high-elevation sites have cooler air temperatures, we found that mean substrate temperatures were similar between low- and high-elevation sites. Correspondingly, FID was uncorrelated with substrate temperature ($r < 0.15$, $P > 0.3$).

Display behavior

We observed 109 individuals for an average of 55.7 ± 7.8 (SD) min for a total of 101.2 h of observation. We found evidence

of divergence in display behavior in the CC, but not the SB (Table 3, Fig. 5). The proportion of time spent displaying is low overall. In the CC, however, we observed that display rates were higher at low elevation (0.032 ± 0.019) than at high elevation (0.011 ± 0.019). Although lizards spent less time overall displaying at high elevation in the CC, both the dewlap rate and the pushup rate were greater at high elevation than low elevation (Table 3, Fig. 5), meaning that high-elevation lizards were packing more dewlaps and pushups into their displays per unit time. Dewlap rate and pushup rate in the SB sites appear to be qualitatively similar to those observed at low, rather than high, elevation in the CC. In contrast, the time spent displaying at the SB sites is more similar to that observed at high elevation in the CC.

Locomotor behavior

The proportion of inactive lizards (MPM < 0.20) with elevation in the CC was not significantly different (Fisher's exact test, $P = 0.56$), but the proportion of inactive lizards was significantly higher at low elevation in the SB (Fisher's exact test, $P = 0.023$) (Table 4). Among active lizards, MPM in the CC or the SB was not significantly different (CC: $t = 0.52$, $df = 35.8$, $P = 0.61$; SB: $t = -0.59$, $df = 3.7$, $P = 0.59$), although the statistical power to detect differences in the SB is low because

TABLE 3. TEST STATISTICS SHOWING DIVERGENCE IN DISPLAY BEHAVIOR WITH ELEVATION IN THE CORDILLERA CENTRAL BUT NOT THE SIERRA DE BAORUCO.

	Cordillera Central			Sierra de Baoruco		
	df	<i>t</i>	<i>P</i>	df	<i>t</i>	<i>P</i>
% Time displaying	51.97	4.66	<0.0001	35.47	0.54	0.60
Dewlap rate ^a	28.09	4.43	<0.001	32.18	0.16	0.87
Pushup rate ^b	28.64	2.43	0.021	18.72	1.54	0.14

^aDewlap rate was calculated as the number of dewlaps divided by the observation length (min).

^bPushup rate was calculated as the number of pushups divided by the observation length (min).

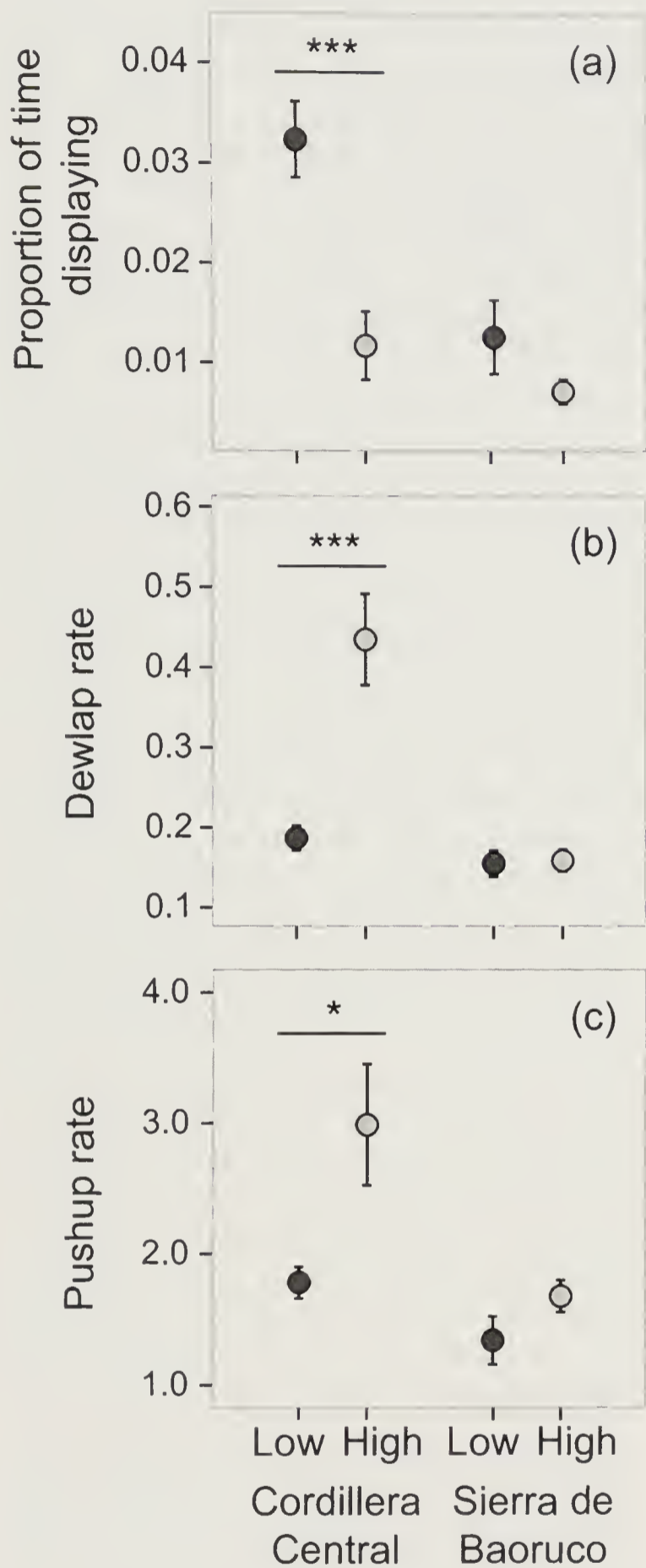


Figure 5. Mean proportion of (a) time spent displaying (display time [min]/observation length [min]), (b) dewlap rate (dewlap number/display time [min]), and (c) pushup rate (pushup number/display time [min]) at low elevation (black circles) and high elevation (gray circles) in the Cordillera Central and Sierra de Baoruco. Error bars represent one standard error. * $P < 0.05$; *** $P < 0.005$.

of small sample size at low elevation. Walk, run, and jump frequency for active lizards are similar across all sites (Table 4).

DISCUSSION

Behavioral patterns within Caribbean anole ecomorphs are well-established (Losos, 2009; Johnson et al., 2010), but these studies have been primarily restricted to a single macrohabitat (i.e., lowland tropical forests). Nonetheless, previous authors have noted that behavioral divergence within ecomorphs across macrohabitats should occur, although empirical studies have been scant (Johnson et al., 2008; Ord et al., 2013). Here, we found that some aspects of behavior (basking and flight initiation distance) shifted predictably with elevation in high-elevation lizards, but display behavior showed mixed patterns, and locomotor behavior did not change.

At high elevation, *A. armouri* and *A. shrevei* used more exposed perches with less canopy cover than *A. cybotes* at low elevation (Table 2). This finding supports qualitative field observations from numerous other studies (Hertz and Huey, 1981; Muñoz et al., 2014; Conover et al., 2015; Muñoz and Losos, 2018). We confirm observations from previous studies that the montane *A. armouri* and *A. shrevei* spent nearly all of their time basking (Hertz and Huey, 1981; Muñoz et al., 2014; Conover et al., 2015), whereas lowland populations of *A. cybotes* spent the majority of their time in the shade (Fig. 3). This observation is consistent with habitat use: by perching in open habitats at high elevation, the lizards can readily raise their body temperature, which is important in their relatively cold environments (Table 1). Conversely, *A. cybotes* might choose shady perches to prevent overheating in warm lowland areas (Muñoz et al., 2014).

The use of open perches—as we observed in both montane cybotoids—is often associ-

ated with greater FIDs (Martín and López, 1995; Schulte et al., 2004; Cooper and Wilson, 2007). Consistent with this expectation, we found that both *A. armouri* and *A. shrevei* displayed heightened levels of wariness, as assessed by FID, compared with low-elevation *A. cybotes* (Fig. 4). One potential mechanism underlying this finding could be that colder air temperatures at high elevation favor longer escape distances because of impaired performance (Rand, 1964b; Rocha and Bergallo, 1990; Smith, 1997; Cooper, 2000); however, previous studies report that mean body temperatures of *A. shrevei* and *A. armouri* differ little from those of low-elevation *A. cybotes* (Hertz and Huey, 1981; Muñoz et al., 2014), and we found no correlation between substrate temperature (our proxy for body temperature) and FID. Alternatively, the open habitat structure at high elevation might favor increased FID because of increased conspicuousness to predators or increased distance to refuges (Martín and López, 1995; Blázquez et al., 1997; Diego-Rasilla, 2003; Schulte et al., 2004; Vervust et al., 2007; Cooper and Pérez-Mellado, 2012). The behavioral shift to more open basking sites that buffer the montane cybotoids from cold temperatures (Muñoz and Losos, 2018) may at the same time expose them to increased predation risk.

Adaptation to cold environments typically involves slower growth, delayed maturation, and investment in fewer, larger offspring (Angilletta, 2009). Female *A. shrevei* retain their eggs significantly longer than *A. cybotes* (Huey, 1977), which should increase inter-clutch interval and decrease fecundity compared with their low-elevation counterparts. Perhaps to accommodate their reduced reproductive output or their greater biomechanical impairment (bulkier eggs held for longer periods of time), high-elevation lizards may use behavioral strategies (i.e.,

increased wariness) to mitigate risk and enhance annual survivorship. Further study is needed to disentangle the potential contributions of habitat openness, life history, and predation pressure to this pattern.

We further predicted that wariness in montane lizards would include a reduction in display time. We found that display behavior differed between high- and low-elevation lizards in the CC, but not in the SB (Table 3). In the CC, lizards at high elevation spent less time displaying than lizards at low elevation (Fig. 5). Reducing the frequency and duration of broadcast displays and selectively decreasing conspicuous display elements are common responses to increased predation risk (Endler, 1987; Candolin, 1997; Bailey and Haythornthwaite, 1998). Although we lack evidence on whether predation risk is higher in montane habitats, we suspect that lizards in more open habitats are likely to be more conspicuous to aerial predators. Although *A. shrevei* displayed less often than low-elevation lizards in the CC, those displays had higher dewlap and push-up rates (Fig. 5), which might reflect a tradeoff between a constraint on display duration and the need to convey information embedded in display elements. The number of pushups in a display, for example, is known to correlate with endurance in *Anolis cristatellus* (Leal, 1999); hence, a shorter display with the same number of pushups might convey the same message while also minimizing risk.

It is also possible that the displays are adapted to differing visual environments or different spectral sensitivities (Endler, 1992; Leal and Fleishman, 2002; Ord et al., 2007; Fleishman et al., 2009) and that these may differ between the CC and SB. Habitat openness is a gross indicator of differences in the visual environments, but careful measurement of the visual environment across both mountain chains and a more

TABLE 4. MOVEMENTS PER MINUTE (MPM) AND WALK, RUN, AND JUMP FREQUENCY (MEAN \pm SD) IN THE CORDILLERA CENTRAL AND SIERRA DE BAORUCO.

Mountain Range	Elevation	<i>n</i> ^a	MPM	% Walk	% Run	% Jump
Cordillera Central	Low	19 (25)	0.57 \pm 0.28	0.69 \pm 0.14	0.07 \pm 0.08	0.24 \pm 0.13
	High	20 (30)	0.63 \pm 0.35	0.76 \pm 0.11	0.06 \pm 0.07	0.17 \pm 0.12
Sierra de Baoruco	High	15 (31)	0.37 \pm 0.16	0.74 \pm 0.19	0.06 \pm 0.09	0.20 \pm 0.14
	Low	4 (23)	0.44 \pm 0.24	0.76 \pm 0.18	0.15 \pm 0.14	0.10 \pm 0.08

^aNumber of active lizards (MPM \geq 0.20 used in analysis) out of the total number of lizards observed (in parentheses).

detailed study of signal properties are required to test these hypotheses (Leal and Fleishman, 2004). One more possibility is that another aspect of visual displays such as head-bobs (which we could not distinguish from pushups during observations) might vary with habitat openness. For example, in the presence of predators, *A. sagrei* alter head-bob displays (Steinberg et al., 2014). Future work that explicitly considers light environment, predation pressure, and social context for displays (e.g., territoriality versus mating) can help elucidate the factors shaping display behavior within ecomorphs.

Finally, we predicted that heightened wariness in high-elevation lizards would result in fewer movements than low-elevation lizards in response to utilizing more open habitats. However, locomotor behavior did not differ in any substantial way among populations (Table 4). This result suggests that locomotor behavior might be relatively stable within ecomorph classes, even across substantially different macrohabitats (Moermond, 1979; Losos, 1990), although Kahrl et al. (2018) found that movement rates differed between *A. cybotes* (0.4 MPM) and two more distantly related cybotoids, *Anolis marcanoi* and *A. longitibialis* (both with \sim 0.1 MPM). Numerous factors beyond macrohabitat may thus influence variation in locomotor behavior.

In the case of the cybotoid anoles, macrohabitat is a strong predictor for basking behavior and escape behavior. Macrohabitat

may also sometimes influence aspects of display behavior. The behavioral differences observed across sites within this ecomorph encompassed a wide range of behavioral variation. Vanhooydonck et al. (2007) reported escape distances of 1–1.5 m in various trunk-ground anole species (*A. cristatellus*, *A. cooki*, *A. gundlachi*, and *A. sagrei*), consistent with our observations of *A. cybotes*. In contrast, mean escape distances in *A. armouri* and *A. shrevei* exceeded 3 m, and many high-elevation lizards fled when researchers were still 5–10 m away. Low-elevation lizards frequently allowed researchers to get within a meter before attempting to flee. The variation in FID that we measured within the cybotoids mirrors the variation generally observed among ecomorphs (range: 1–4 m) (Cooper, 2006). For display behavior, the values obtained in this study for proportion of time displaying and dewlap rate span the range observed across 15 species belonging to five ecomorphs (Johnson, 2007; Johnson and Wade, 2010). Nonetheless, behavior is a highly flexible phenotypic trait, and one that can be highly dependent on context. These observed behavioral shifts could reflect fixed differences between *A. cybotes* and the two montane forms, or clinal shifts with elevation. Examining these same behaviors at intermediate elevations on Hispaniola would help disentangle these two possibilities.

The ecomorph concept in *Anolis* lizards is defined by the association between structural

microhabitat and morphology, with members of the same ecomorph sharing several morphological, behavioral, and ecological traits (Losos, 2009). Whereas morphological diversity within ecomorphs is by definition limited (Losos, 1990), we find that high- and low-elevation cybotoids nonetheless diverge in various ecological and behavioral features. Our understanding of anole evolution can be strengthened and expanded by continued study of within-ecomorph divergence along environmental clines.

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